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RELATIONSHIPS BETWEEN EOLID (MOLLUSCA, NUDIBRANCHIA) RADULAR MORPHOLOGY AND THEIR CNIDARIAN PREY***

KEY WORDS: Nudibranchs; Cnidarians; Radular morphology; Trophic relationships.

Abstract

Eolids, among nudibranchs, usually feed on cnidarians, mostly on hydroids. The assessment of the relations between the morphological characteristics of the prey and the morpho-functional aspects of the radular structure of seventeen families of eolids has been attempted from data available in the literature.

Riassunto

Gli eolidiacei, tra i nudibranchi, predano generalmente cnidari, ed in particolare idrozoi. L'analisi del rapporto tra morfologia radulare e preda presenta, tuttavia, notevoli difficoltà interpretative. Specie con radule triseriate, ad esempio, predano indifferentemente sia idroidi tecati che atecati o la stessa preda è attaccata da specie con formule radulari diverse. In questi casi, più che la morfologia della radula è importante il comportamento predatorio della specie, comportamento ancor oggi assai poco conosciuto. Una buona convergenza morfologica esiste invece tra le radule delle famiglie che predano, rispettivamente, specie neustoniche ed attiniari.

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Introduction

The diet of nudibranch molluscs shows a general tendency of the species to select a given type of prey. TODD (1981), in a review of nudibranch ecology, distinguished four trophic groups: sponge-grazers (dorids), bryozoan-grazers (mainly dorids), hydroid-grazers (eolids) and «miscellaneous» groups, including representatives of all four suborders preying upon other different taxa. Recently CATTANEO VIETTI & BALDUZZI (in press) studied this

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relationship in dorids. Even though eolids feed mostly on hydrozoans and anthozoans (mainly actinians) some of them (e.g. *Facelina annulicornis, F. coronata, Phidiana crassicornis, P. pugnax*) are euryphagous and can attack other opisthobranchs or small invertebrates. *Calma glaucoides* feeds on teleost eggs, and *Favorinus* spp. on invertebrate eggs. Some neustonic species (e.g. *Glaucus atlanticus, Glaucilla* spp. and *Fiona pinnata*) feed on planktonic cnidarians, molluscs or stalked barnacles.

Eolids act as a controlling factor in the development of hydroid populations, being able to completely deplete them, mainly at the end of the seasonal cycles of the species (Barange *& al.*, in press; McLeod & Valiela, 1975). The feeding intensity of an eolid can be high: *Tenellia adspersa* can destroy up to 100 adult hydranths of *Perigonimus megas* in 24 hr (Turpaeva, quoted by Roginskaya, 1970).

In this paper we aim to point out the relationship between morphological characters of the prey and of the radular structure in 17 families of eolids, especially those feeding on hydroids. The feeding preferences of actinian-predators were recently studied by Tardy (1969), Waters (1973), Edmunds *& al.* (1974), Moreteau (1977), Hall *& al.* (1982), and Edmunds (1983).

Material and methods

The bulk of data was drawn from the literature: we have used the data reported by Barletta (1976), Behrens (1980), Bouchet & Tardy (1976), Clark (1976), Edmunds & Kress (1969), Farmer (1980), Gosliner (1979), Gosliner & Griffiths (1981), Haefelfinger (1960), Kuzirian (1979), MacDonald & Nybakken (1978; 1980); Miller (1961; 1971; 1977), Ros (1975; 1978), Rudman (1979; 1980; 1981; 1982), Schmekel & Portmann (1982), Salvini-Plawen (1972), Swennen (1961), Tardy (1969), Thompson & Brown (1984), Todd (1981).

The data concerned over 130 species which feed upon over 20 families of hydroids, excluding anthozoans and other less important taxa. To facilitate the interpretation the data were divided according to the families and the classifications proposed by Schmekel & Portmann (1982) and Thompson & Brown (1984) for nudibranchs, and by Bouillon (1985) for hydroids, are adopted.

Data were considered from a qualitative point of view (presence/absence of a prey in the diet of every radular group).

Results

A large part of the eolids feeds on hydroids (Tab. 1). Also primitive Notaeolidiidae, with an unusual pluriseriate radula (2.5.1.5.2.), feeds on athecates hydroids (probably Capitata), according to VAYSSIERE's (1905) drawings of the nematocysts found in the cerata. Most of the advanced families of eolids have continued this specialisation on hydroid prey.

No strong correlation between radular type (uni-, tri-, and multiseriate) and hydroid type exists: eolids with both uniseriate and triseriate radulae were reported to feed on both thecate and athecate hydroids. (Tab. 2).

The triseriate Eubranchidae seem to prefer thecates whereas the triseriate Pleuroprocta (Flabellinidae, Cumanotidae, Pleurolidiidae) tend to feed on athecates. The Facelinidae have a varied and complex diet (some species are euryphagous), but prefer athecates. The Tergipedidae, apart from specialized species as *Cuthona nana* feeding on Hydractiniidae (CHRISTENSEN, 1977), *Cuthona poritophages* and *Phestilla* spp. feeding on scleractian coral (RUDMAN, 1979; 1981), shows a tendency to feed on thecates. The doubtful genus *Catriona* seems to prefer athecates.

The monospecific Fionidae and Calmidae feed, respectively, on a diet range of neustonic species and teleost eggs, whereas the paucispecific psmammophilous family Pseudovermidae preys on the athecate Euphysidae and on the actinulid Halammohydridae.

Finally Aeolidiidae, Pteraeolidiidae and some Herviellidae prey on actinians.

Table 1
Percent frequences of preys in the diet of aeolid families according to references listed at pag. 2.

		Rad. type	Athecata	Thecata	Eggs	Anthozoa	Others
	Notaeolidiidae	multiseriate	100	—	—	—	—
HETEROPROCTA	Flabellinidae	triseriate	73	25	—	—	2
	Cumanotidae	triseriate	100	—	—	—	—
	Pleurolidiidae	triseriate	100	—	—	—	—
	Glaucidae	uniseriate	50	—	—	—	50
	Facelinidae	uniseriate	63	25	—	—	13
	Favorinidae	uniseriate	22	22	44	—	12
	Pteraeolididae	uniseriate	—	—	—	100	—
	Herviellidae	uniseriate	—	33	—	67	—
	Aeolidiidae	uniseriate	—	—	—	100	—
ACLEIOPROCTA	Piseinotecidae	uniseriate	50	50	—	—	—
	Eubranchidae	triseriate	15	85	—	—	—
	Pseudovermidae	triseriate	100	—	—	—	—
	Tergipedidae	uniseriate	43	50	—	7	—
	Embletoniidae	uniseriate	50	50	—	—	—
	Fionidae	uniseriate	67	—	—	—	33
	Calmidae	uniseriate	—	—	100	—	—

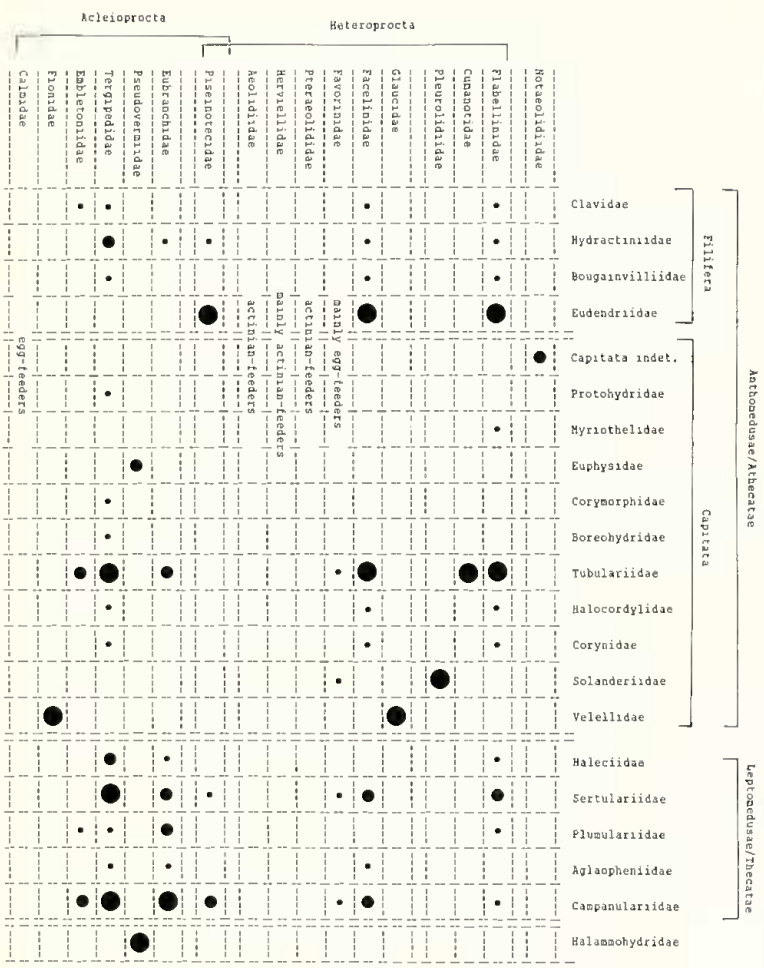
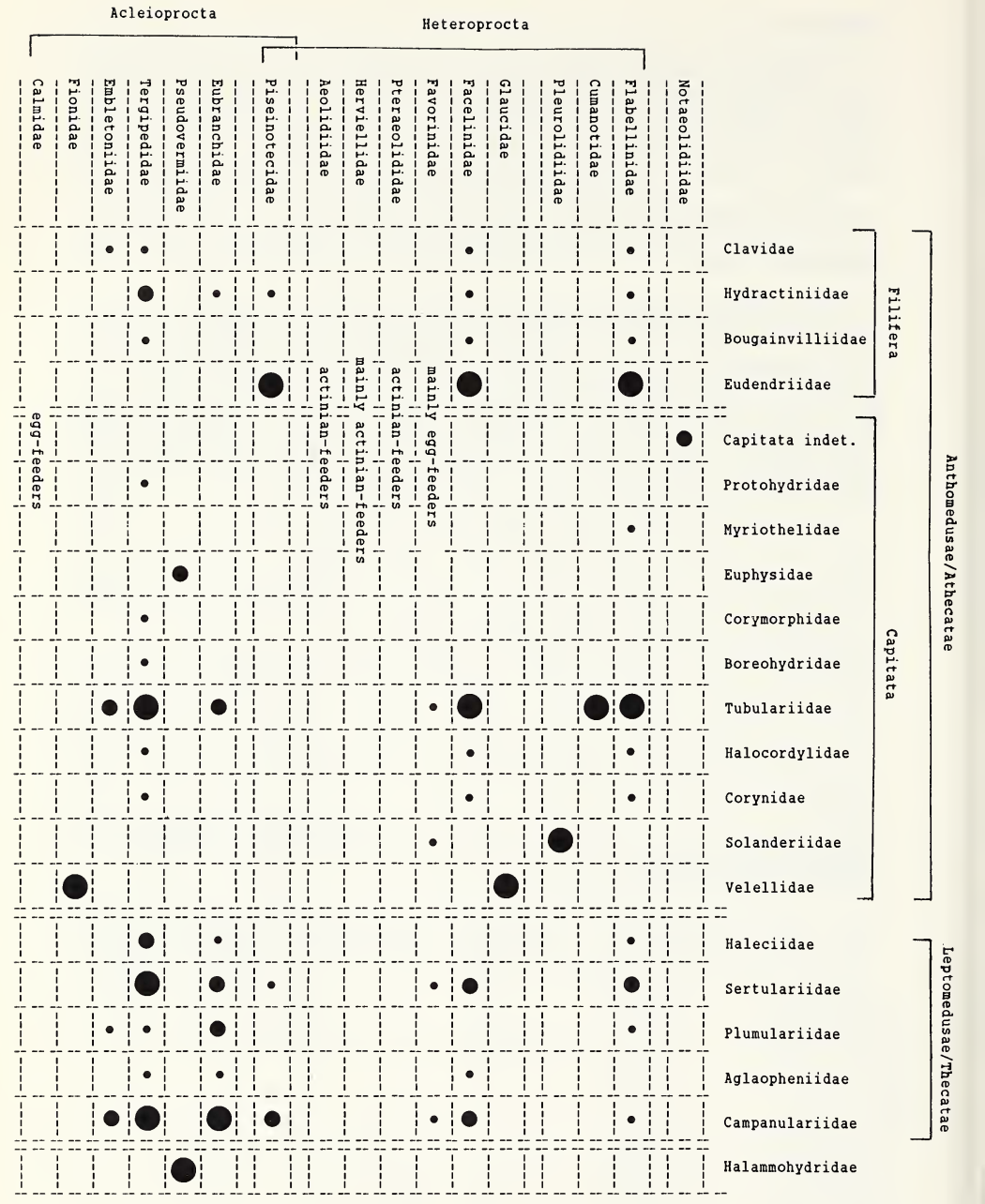


Table 2
Food trends of hydroid-feeder eolids according to references listed at pag. 2.
● = main food
● = secondary food
• = occasional food



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Discussion

As already suggested by Nybakken & McDonald (1981), the available data make the correlation between radular shape and diet difficult. The radular patterns do not allow any discrimination between thecate and athecate feeders. Nybakken & McDonald (1981) proposed two different feeding tactics according to radular types: species with uniseriate radulae feed by puncturing the perisarc of the prey, then ingesting the coenosarc, while species with triseriate radulae tend to feed directly on naked hydranths or gonophores.

It is possible, however, to find cases in which the differences between triseriate and uniseriate radulae are less clearly defined. *Flabellinopsis iodinea*, for instance, manipulates the hydranths of *Eudendrium ramosum* with the lips so as to put them into a suitable position for the jaws to grasp; the hydranths are torn from the stalk as a result of 3 or 4 violent contractions of the body and are then drawn into the mouth by radular action (McBeth, 1971). *Cratena peregrina* shows a completely different behaviour to feed on the hydranths of *Eudendrium racemosum*. The hydranths, in fact, are attacked from one side of their base until all the hydranth body is ingested, the stalk is then cut and also the tentacles pass into the mouth. *Flabellinopsis iodinea* has a triseriate radula, whereas *Cratena peregrina* has a monoseriate one. Both feed on hydranths of congeneric species but adopt two different feeding strategies.

Morever it is apparent that many species feed both on thecates and on athecates, so that the same radular type may be used for preys with different features.

On the contrary, a strict relationship exists between Aeolidiidae, Pteraeolidiidae and some Herviellidae reported to prey on actinians: they have a pectinate, broad and uniseriate radula. The tooth of the tergipedid *Phestilla*, feeding on scleractinian corals (Rudman, 1981; 1982a), shows long pointed denticles with the tips all approximately at the same level, perhaps due to morphological convergence with the actinian-feeder genera.

Another good resemblance appears to be between Glaucidae and Fionidae strong cuspidated teeth: both families feed on neustonic species.

The apparent lack of homogeneity in many of the data recorded from the literature possibly reflects insufficient observation. The simple record of the species on which a given nudibranch was collected gives only a rough indication about its diet, especially if the feeding technique has not been carefully studied.

Other points are anyway relevant in the study of trophic relations between nudibranchs and hydroids.

— The big colonies of some hydroid species are often covered by epibiotic hydroids of smaller size. These are not easily detectable in situ, but could be the object of predation. The nudibranch should be taken together with its possible prey, the cnidome of the prey should be studied and compared with the clepto-cnidome of the nudibranch, to verify if they match.

If they don't, another prey should be searched on. Direct observation of feeding, however, is the definitive way to assess a diet.

— Diets are possibly related with the age of the predator (Todd, 1983). The juveniles, in fact, may begin feeding on small thecate hydranths and, once adult, may pass to the bigger hydranths of athecates. Thecate hydroids, besides having smaller hydranths than athecates, generally have also smaller nematocysts, which could be easier to pack in the cnidosac of juvenile nudibranchs. *Coryphella pedata*, for instance, feeds on athecates when adult, whereas young stages have been recorded feeding on the thecates *Obelia geniculata* and *Sertularella gayi* (Garstang, 1890 quoted by Thompson & Brown, 1984).

— Many hydroid species are seasonal, so that the same nudibranch could feed on different species in the different periods of the year.

— SStrong differences may be evidenced in the diets of populations of the same species living in far apart areas: *Coryphella lineata* is reported to feed on Eudendriidae in the Mediterranean, and on Tubulariidae in the Atlantic.

— Preys must be identified at specific level. The genus *Eudendrium*, for instance, comprises species with big nematocysts and species with small ones, some species have a pseudohydrotheca, others have cnidophores. These features could require different specializations of the predators.

— The choices of nudibranchs could be influenced by experimental conditions when studies are done in the laboratory.

— Some radular types allow a generalist diet, as evidenced by Cattaneo Vietti & Balduzzi (in press) for dorids.

A general outcome of the present review is that the feeding biology of eolid nudibranchs is far from being completely understood. Further approaches to this problem should carefully consider also the biology of the prey species.